

SOME CONSEQUENCES OF SEXUAL DIMORPHISM: FEEDING
IN MALE AND FEMALE FIDDLER CRABS,
UCA PUGNAX (SMITH)

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The males of *Uca pugnax* (Smith), a fiddler crab species found along the coast of the northwest Atlantic Ocean, have one large chela used for mating displays, sound production, and aggression (Altevogt, 1955; Crane, 1941, 1943, 1967; Pearse, 1912; Salmon, 1967), and one small feeding chela. The female fiddler crab has two small feeding chelae. The crabs feed by picking up bits of mud and detritus from their habitat using the feeding chelae (Miller, 1961).

Kingsley (1888), Hyman (1920), Swartz and Safir (1915), Pearse (1912), Altevogt (1955) and Ono (1968) observed that females show more feeding motions than males, presumably because both feeding claws can operate alternately with almost continuous delivery of food particles to the mouth. If metabolic demands of both sexes are similar, the sexual dimorphism in the feeding claws must have forced the males to evolve some compensatory mechanisms such that food assimilation equals that of females.

Male fiddler crabs could increase food ingestion by having faster feeding motions, by feeding for a longer period of time than females, by feeding on larger mouthfuls or by having a higher assimilation efficiency of the food they do ingest. This paper first attempts to determine if there are any differences in metabolic rates, food intake, fecal production or digestive efficiency between male and female *U. pugnax* and then ascertains whether differences in duration of feeding or morphological dimorphisms involved in feeding exist between the two sexes.

METHODS

All crabs used in this study were collected at Great Sippewissett marsh in Falmouth, Massachusetts, in early fall, were brought to the laboratory and kept in seawater tables at room temperature. Activity cycles in fiddlers may last as long as one week away from water (Bennett, Shriner and Brown, 1967). All experiments were conducted at times corresponding to low tide, the time of maximum activity in the field.

Respiratory rates were measured with an oxygen electrode and chart recorder connected to a respiration chamber consisting of a 250 ml plastic cylinder stoppered at both ends. Demeusy (1957), Teal (1959), Vernberg (1959), Vernberg and

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Vernberg (1966) and Teal and Carey (1967) have previously measured respiration in *Uca*. Crabs in the present study were grouped by sex and size. Two crabs of the same sex and differing by no more than 0.25 mm in carapace width were placed in the seawater-filled chamber. A perforated stopper was pressed down into the chamber until all bubbles were excluded. The electrode was then inserted through the perforation. The water was stirred to avoid saturation of the electrode (Kanwisher, 1962). Temperature was measured before and after the 15 min. period during which the crabs were held in the chamber for respiration measurements.

Dry weight of males and females were obtained. To ensure reasonable comparisons the weight of the sclerotized parts of one of the chelae was subtracted from total weight. This eliminated the bias due to the enlarged male claw. The sclerotized portion of the chelae was measured by carefully removing muscle tissues and weighing the dried hard parts.

Size-matched crabs were starved two days and placed in individual fingerbowls to measure the amount of sediment ingested by male and female crabs of similar size. Three grams of marsh mud resuspended in water were placed with the crabs in 1 cm of seawater. The crabs were left undisturbed for six hours after which they were removed, along with any fecal pellets deposited. The remaining mud was redried and weighed.

The number of fecal pellets produced by crabs per unit time and the amount of organic matter in the pellets were measured to provide some idea of the amount of food processed and the efficiency with which organic matter contained in ingested mud was assimilated by males and females. About 20 g of wet marsh mud were placed in a fingerbowl containing seawater and offered to 3 male and female crabs of three size classes. The crabs were allowed to feed for five days under a regime of 12 hrs of dark and 12 hrs light. Fecal pellets were collected every three hours.

The volumes of the fecal pellets as well as their dry weight were obtained. Whole fecal pellets were then combusted in a muffle furnace at 500° C for 24 hrs to allow the calculation of percent organic matter. The organic content of the mud on which the crabs fed was also measured.

Further measurements of the number of pellets were obtained by cutting 4 cm deep, 20 cm diameter cores of marsh turf, placing them in fingerbowls, and allowing crabs to feed on the surface sediments. Field measurements of pellet production were carried out by first locating single-entrance burrows by pumping seawater through the entrance and observing if water flowed out of any neighboring burrows. Once single entrance burrows were found, 6 inch aluminum flashing was used to construct a circular enclosure 20 cm in diameter. The marsh vegetation was removed from the enclosure and all fecal pellets were removed from the sediment prior to starting. The number of pellets was counted at feasible intervals over a 24 hr period.

The number of feeding motions of male and female crabs was recorded by observing individuals feeding on marsh sediment on a shallow seawater table for two minutes. Wooden barriers with narrow viewing slots were erected around the tables to prevent disturbing the crabs. Feeding motions consisted of a single chela moving from the sediment to the buccal cavity.

TABLE I

Regression lines fitted to values of partial pressure of oxygen (mm Hg) in the respiration chambers during a 15 min period for male and female crabs of various size classes. Initial temperature was 20° C, final temperature 21° C. Mean weights were calculated as dry weight minus 88.5% of the larger claw.

Carapace width class (mm)	Male crabs	Female crabs
13.3-13.5	16.0-0.08 × 0.25	16.3-0.08 × 0.26
13.8-14.0	15.9-0.08 × 0.27	15.7-0.10 × 0.31
14.0-14.3	16.0-0.11 × 0.30	16.1-0.11 × 0.31
14.5-14.8	15.6-0.15 × 0.32	15.6-0.12 × 0.34

The duration of feeding was measured by recording feeding activity of crabs placed in three shallow seawater tables. Each table was observed for 15 min repeating the sequence of observations five times until 75 min of observation per table were completed. Each observation period was divided into fifteen 1 min. segments. If a crab moved its feeding claws from the mud to its buccal cavity during any 1 min interval, a feeding unit was recorded. The feeding units for each crab were then summed for the five observation periods.

To obtain an indirect measure of food-gathering ability the length of the feeding chelae and the width of the flat ventral tip of the dactyl of the feeding claw were measured. The carapace width of each specimen was recorded as well.

RESULTS

Metabolic rates and food processing

There were no significant differences in the rates at which male and female crabs of similar size depleted oxygen (*t* tests on the slopes of the regression lines, $P > 0.05$, Table I). The very slight differences in weight between males and females were not significant.

The amount of mud ingested by starved male and female crabs did not differ significantly when tested with a paired *t* test (Table II).

The number of fecal pellets produced by male and female crabs (Table III) was variable but a two-way analysis of variance of the data from the laboratory

TABLE II

Amount of sediment ingested by starved U. pugnax during a six-hour feeding period in the laboratory.

Carapace width (mm)	g of sediment ingested	
	Female crabs	Male crabs
18.1	0.47	0.35
12.6	0.50	0.47
22.7	0.19	0.37
$\bar{x} \pm \text{s.e.}$:	0.39 ± 0.10	0.40 ± 0.04

TABLE III

Number of fecal pellets produced by individual crabs per 24 hrs, feeding on loose mud obtained from the surface of Great Sippewissett marsh, in the surface of a core of marsh sediments taken into the laboratory and within field enclosures. The values in parenthesis are the number of individual crabs involved.

	Size of crabs expressed as carapace width (cm)	Mean No. of fecal pellets/24 hrs ± st. error	
		Female crabs	Male crabs
Crabs feeding on loose detritus in lab:	0.8-0.9	172 ± 58 (2)	119 ± 11 (2)
	1.2-1.3	53 ± 6 (2)	123 ± 31 (2)
	1.6-1.7	47 ± 13 (2)	98 ± 33 (2)
Crabs feeding on surface of marsh core in the lab:	1.2	129.5 ± 2.5 (1)	155.5 ± 23.5 (1)
	1.3		174.5 ± 4.5 (1)
	1.4		117.6 ± 3.5 (1)
Crabs feeding on marsh surface within field enclosures:	0.6	176 (1)	
	1.2-1.3	143.5 ± 37.5 (2)	157.2 ± 15.2 (4)
	1.6		177.5 ± 3.5 (2)
	1.9-2.1	142 (1)	110.8 ± 11.0 (4)

crabs fed on loose detritus showed that neither sex nor size of crabs significantly affected the number of fecal pellets obtained within 24 hrs. No differences are seen in the values obtained for the field measurements or the laboratory crabs feeding on the surface of a marsh core (Table III).

The volume and weight of fecal pellets (Table IV) were affected significantly by size of crabs ($F = 29.9$ and 4.15 respectively, both with 2 and 6 d.f.) but not by sex ($F = 0.8$ and 4.5 respectively, with 1 and 6 d.f.). The amount of organic matter (Table IV) in the pellets is not significantly related to either size or sex of crabs. There was no significant interaction between sex and size of fiddler crabs in any of these experiments.

These results suggest that male and female fiddlers did not have different metabolic demands and that the amount of bulk food processed by each sex is

TABLE IV

Volumes, weights and percent organic matter of fecal pellets for fiddler crabs. Six to 15 pellets were used from each of two crabs in each treatment combination. Tabled values are mean ± standard errors.

Size of crabs expressed as carapace width	Female crabs			Male crabs		
	Vol/pellet (10^{-5} cm ³)	Wt/pellet (10^{-5} g)	% organic matter	Vol/pellet (10^{-5} cm ³)	Wt/pellet (10^{-5} g)	% organic matter
0.8-0.9 mm	56 ± 15	33.1 ± 3.1	31 ± 0.2	83 ± 15	46.3 ± 2.8	34.6 ± 1.1
1.2-1.3 mm	172 ± 22	77.3 ± 23.3	34.5 ± 0.9	222.5 ± 30.5	78.9 ± 7.4	29.2 ± 4.1
1.6-1.7 mm	364.5 ± 40.5	112.8 ± 1.2	35.1 ± 0.7	349.5 ± 33.5	150.8 ± 1.8	32.8 ± 0.1

TABLE V

Number of feeding motions per 2 min observation period. Tabled values are mean plus or minus standard errors.

Carapace width	No. of individuals observed	No. feeding motions per 2 min	
		Females	Males
13-14 mm	16 males, 16 females	64.6 ± 2.0	33.0 ± 1.1
14-15 mm	15 males, 15 females	68.9 ± 2.2	38.5 ± 1.2

similar. Further, neither sex was more efficient at removing organic matter out of the ingested sediment. The organic content of the sediment on which the crabs fed was 23.7%, considerably lower than that of the pellets. This probably indicates selective feeding on particles of high organic content. There is a possibility that male crabs are more selective than females, choosing only the richest particles, but we have no evidence for this.

Feeding behavior

Table V shows that female *U. pugnax* carry out almost twice as many feeding motions as males during comparable spans of time. This was due to almost simultaneous feeding with two feeding appendages in the female. Males did not therefore use faster feeding motions to compensate for using only one feeding claw. Although there was considerable variation among individual crab, males did feed roughly twice as long as females, since male crabs scored about twice the feeding units awarded to females (Table VI).

Feeding morphology

The length of the feeding chela of males and females do not differ for specimens of comparable carapace width (Fig. 1). However, the width of the small flat ventral area on the tip of the dactyl of feeding claws is larger in males than in females (Fig. 2). The slopes of the regression lines are similar but the values for male *U. pugnax* lie above those for females for any comparable carapace width. This

TABLE VI

Number of feeding units recorded for a period of 75 minutes and three different seawater tables. Six male and female crabs were used in each table. See text for scoring of feeding units.

Table no.	Female crabs		Male crabs		Ratio male/female feeding units
	Range of carapace widths (mm)	No. of feeding units	Range of carapace widths (mm)	No. of feeding units	
1	15.1-17.4	6.8 ± 2.7	15.7-20.9	13.0 ± 2.7	1.9
2	14.2-18.3	7.7 ± 2.3	14.8-17.2	16.8 ± 4.6	2.2
3	14.0-17.1	3.7 ± 0.6	14.7-19.5	7.8 ± 1.1	2.1

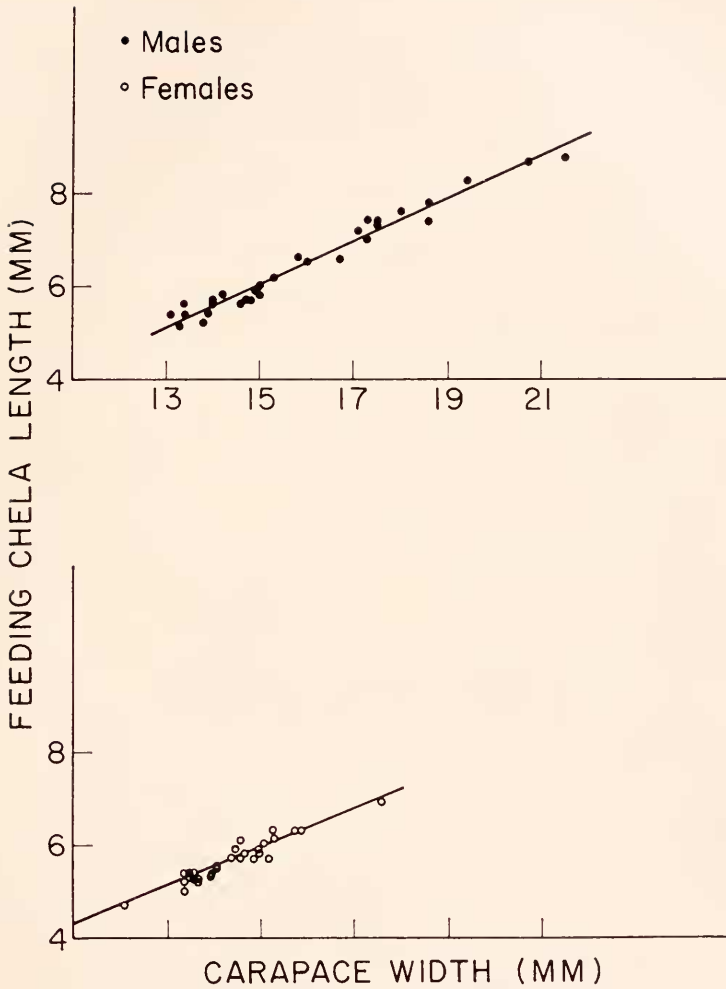


FIGURE 1. Length of feeding claws versus carapace width in male and female *Uca pugnax*. The lines show the calculated regression line for the points.

might make it possible for males to obtain larger mouthfuls per feeding motion than females.

DISCUSSION

Our results suggest that male and female fiddler crabs have similar nutritional demands, food-processing abilities, and digestive efficiencies. Since males have only one functional feeding claw, the number of feeding motions is half that observed in female *U. pugnax*. Males seem to compensate by extending the duration of feeding behavior. In the field feeding occurs mainly at low tide during daylight

(Ono, 1968, and our own observations). We have observed males feeding underwater in Massachusetts and Teal (1958) saw crabs feeding during high tides in Georgia. In the marshes of Buzzards Bay along the coast of Massachusetts, mud flats and grass-covered habitats in which *Uca* feed are exposed for about four hours at low tide. We have observed that as high tide approaches only males are still feeding. This agrees well with our results of prolonged feeding with males.

The two-fold increase in feeding duration would seem to be enough compensation for lack of a feeding appendage. However, the morphology of the feeding claw is such that males may be able to grasp and feed on larger mouthfuls per feeding motion.

Longer feeding periods may expose males to greater predatory mortality. However, in a sample of 713 specimens of *U. pugnax* from Great Sippewissett Marsh there were more males than females present (42.9% females). This sex ratio was very similar to that found by Shanholzer (1973) in a salt marsh in Georgia and is not unusual among marine invertebrates (Wenner, 1972). Data now in preparation from Great Sippewissett show greater mortality of the smaller females than males. The need to repeatedly expose eggs to the flow of well-oxygenated water may increase the exposure of berried females to predatory mortality by forcing females to remain in the relatively unprotected creek banks at high tide. The egg masses also may impede locomotion of females and increase

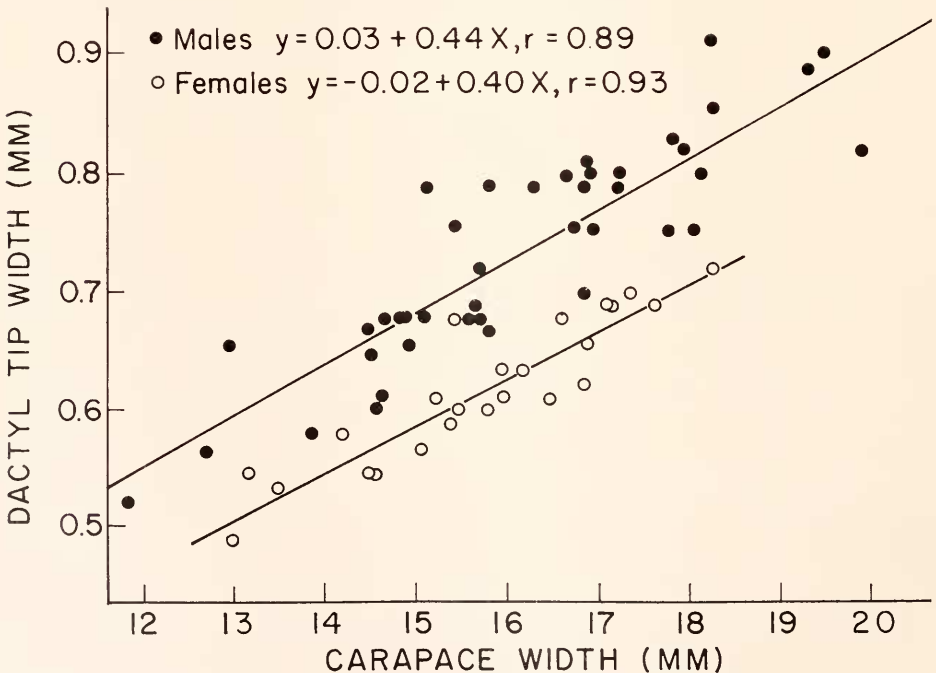


FIGURE 2. Width of the tip of the feeding dactyl versus carapace width in male and female *Uca pugnax*. The lines show the calculated regression line for the points.

their vulnerability to predators (Hyman, 1920). It may be, however, that differential mortality between the sexes does not affect the sex ratios (Leigh, 1970) so that sexual dimorphism does not directly lead to different survivorship rates.

There are no doubt seasonal fluctuations on the metabolic expenditures of male and female crabs related to sexual dimorphism. Males show great activity during breeding displays (Crane, 1958, 1966; Salmon, 1965), while berried females not only produce eggs from late May to early July but must, as already mentioned, care for the egg masses. To fully develop the consequences of sexual dimorphism these changes over time must be considered. This paper merely illustrates that at any one time there are mechanisms operating by which males compensate for the lack of one feeding appendage, and the results also evidence the complex consequences of apparently simple morphological and behavioral differences.

SUMMARY

1. There were no differences in the respiratory rates of male and female *Uca pugnax* of comparable sizes.

2. The amount of salt marsh sediment ingested by starved male and female crabs was similar.

3. The number and weight of fecal pellets produced by male and female crabs were similar, as was the organic matter content.

4. The above suggests that there are minimal differences in food demands and digestive efficiencies between the sexes, yet the enlarged claw of the fiddler crabs cannot be used for feeding. This requires some compensatory mechanism in male crabs.

5. Male fiddlers do show about half the feeding motions per unit time compared to females, but they compensate by feeding about twice as long. This is corroborated by field observations.

6. Further compensation, if needed, could be achieved by the slightly larger holding surface of the feeding claw in males, perhaps allowing the grasping of larger fragments of marsh sediment.

LITERATURE CITED

- ALTEVOGT, R., 1955. Some studies on two species of Indian fiddler crabs, *Uca marionis nitidus* and *Uca anallipses*. *J. Bombay Natur. Hist. Soc.*, **52**: 702-716.
- BENNETT, M. F., J. SHRINER, AND R. A. BROWN, 1967. Persistent tidal cycles of spontaneous motor activity in the fiddler crab, *Uca pugnax*. *Biol. Bull.*, **112**: 267-275.
- CRANE, J., 1941. Crabs of the genus *Uca* from the west coast of Central America. *Zoologica*, **26**: 145-208.
- CRANE, J., 1943. Display, breeding and relationships of fiddler crabs (genus *Uca*) in the field. *Zoologica*, **28**: 217-223.
- CRANE, J., 1966. Combat, display, and ritualization in fiddler crabs (Oxyopodidae), genus *Uca*. *Phil. Trans. Roy. Soc. London Series B.*, **251**: 459-472.
- CRANE, J., 1967. Combat and its ritualization in fiddler crabs (Oxyopodidae) with special reference to *Uca rapax*. *Zoologica*, **52**: 49-77.
- DEMEUSY, N., 1957. Respiratory metabolism of the fiddler crabs *Uca pugilator* from two different latitudinal populations. *Biol. Bull.*, **113**: 245-253.
- HYMAN, O., 1920. Adventures in the life of a fiddler crab. *Ann. Rep. Smith. Inst.*, **1920**: 433-460.

- KANWISHER, J., 1962. Oxygen and carbon dioxide instrumentation. *Mar. Sci. Inst.*, **1**: 334-339.
- KINGSLEY, S., 1888. Something about crabs. *Amer. Natur.*, **22**: 888-896.
- LEIGH, E. G., JR., 1970. Sex ratio and differential mortality between the sexes. *Amer. Natur.*, **104**: 205-210.
- MILLER, D., 1961. The feeding mechanism of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica*, **46**: 89-100.
- ONO, Y., 1968. On the ecological distribution of ocyroid crabs in the estuary. *Mem. Fac. Sci. Kyushu Univ. Ser. E. Biol.*, **4**: 1-60.
- PEARSE, A. S., 1912. The habits of fiddler crabs. *Phillipp. J. Sci. 2D.*, **7**: 113-133.
- SALMON, M., 1967. Coastal distribution display and sound production by Florida fiddler crabs (genus *Uca*). *Anim. Behav.*, **15**: 449-459.
- SALMON, M., 1965. Waving display and sound production in the courtship behavior of *Uca pugilator* with comparisons to *U. minax* and *U. pugnax*. *Zoologica*, **50**: 123-148.
- SHANHOLTZER, S. F., 1973. Energy flow, food habits and population dynamics of *Uca pugnax* in a salt marsh system. *Ph.D. thesis, University of Georgia*, 91 pp.
- SWARTZ, B. AND S. SAFIR, 1915. Natural history and behaviour of the fiddler crab. *Cold Spring Harbor Monogr.*, **8**: 3-23.
- TEAL, J. M., 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology*, **39**: 185-193.
- TEAL, J. M., 1959. Respiration of crabs in Georgia salt marshes in its relation to their ecology. *Physiol. Zool.*, **32**: 1-14.
- TEAL, J. M., AND F. G. CAREY, 1967. The metabolism of marsh under conditions of reduced oxygen pressure. *Physiol. Zool.*, **40**: 83-91.
- VERNBERG, F., 1959. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. II. Oxygen consumption of the whole organism. *Biol. Bull.*, **117**: 163-184.
- VERNBERG, F. AND W. VERNBERG, 1966. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. VII. Metabolic-temperature responses in southern hemisphere crabs. *Comp. Biochem. Physiol.*, **19**: 487-524.
- WENNER, A. M., 1972. Sex ratio as a function of size in marine crustacea. *Amer. Natur.*, **106**: 321-350.